THE HAIR TRACTS IN MARSUPIALS.

PART 1. DESCRIPTION OF SPECIES.

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(Twenty-five text-figures.)

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During the last forty years questions surrounding the phylogenetic significance and causation of hair tracts in mammals have received only sporadic attention. Prior to the pioneer efforts of Kidd (1903, 1920), which began to appear at the turn of the century, very little was known of the arrangement of hair in mammals other than man. Kidd's work, not well received at the time, was accorded only infrequent mention in literature subsequently. The reason for this neglect is not difficult to trace and is most certainly to be found in the presentation of his facts as an example of the inheritance of acquired characters. Schwalbe's work (1911) on some of the Primates is an outstanding contribution to the development of the subject, but the other mammalian groups received only scant attention until, in 1920, Wood Jones commenced to record hair tracts in Australian marsupials. Wood Jones (1924, 1925*a*, 1925*b*, 1941, 1943), like Kidd, is a powerful advocate for Lamarckian explanation, and in the inevitable controversy surrounding the advancement of such a thesis, the use which might be made of the variations in the arrangement of hair tracts in throwing light on questions of phylogeny has largely been lost sight of. The probable taxonomic value of hair arrangement has been exploited in the case of man, and there is a growing literature embodying data which have been gathered in an endeavour to establish characteristics in hair disposition as criteria of race. This refers particularly to the occipital and dorsal whorls (Wood Jones, 1927; Ride, 1932; Gray, 1935). Nevertheless, knowledge of the hair tracts in the Primates is incomplete and discontinuous and the same is true in greater measure of the other mammalian groups. Much of interest which study of hair tracts might yield is obscured by the lack of a reasonably complete picture of their arrangement and distribution within the limits of a single order. The material which forms the basis of this series of contributions should provide such a picture for the Marsupialia.

Terminology.

In general, descriptive terms are employed in the sense given to them by Schwalbe (1911) and in the several papers of Wood Jones.

The *primitive arrangement* of the hair has been variously defined. In the words of Wood Jones (1924), "It may be taken as the nearest approximation to truth to assert that in the primitive mammalian coat the hair is all directed caudad and ventrad upon the trunk and post-axially and distally upon the limbs. Several marsupials fulfil this condition and *Myrmecobius* and *Dasycercus* may be quoted as examples".

The crown-rump length or that of the extended head and body has been given in accordance with the manner in which the specimens lent themselves the more readily to one measurement or the other. In the case of series containing individuals from the same litter and, therefore, approximately equal in size, the measurements given are the average for the individuals concerned.

To avoid unnecessary duplication in the text, wherever possible, one species of a family or smaller grouping has been selected for detailed consideration and the related forms described by reference to it. No attempt has been made, at this stage, to describe the tracts on the elevations and depressions of the lateral surface of the auricle.

The taxonomic nomenclature used is that of Iredale and Troughton's check-list (1934).

Acknowledgements.

The twenty-three species which form the basis of this contribution are, with a single exception, from the collection of embryos of the Australian Museum, Sydney. I am deeply indebted to Mr. E. Le G. Troughton, Mammalogist, for calling my attention to the existence of this excellent and representative material, and to Dr. A. B. Walkom, Director of the Australian Museum, who very kindly made them available to me for study.

Suborder Polyprotodontia.

Family Dasyuridae.

Subfamily Phascogalinae.

Antechinus flavipes flavipes Waterhouse.

Material.—M.4793 part—a litter of seven (crown-rump length about 16 mm.); Wyong, New South Wales; coll. J. H. Wright and W. Barnes, Nov., 1929.

The hair is sufficiently developed for charting on the dorsal and lateral aspects of the head and neck, and along the back except in its caudal third. Hair trend is also discernible on the throat between the mandibles, but elsewhere the growth is insufficient to be of use.

No reversals or other interruptions of the primitive head to tail flow could be detected. There is a tendency for the hairs on the dorsal part of the neck and on the back between the shoulders to flow with a slightly medial inclination.

Antechinus maculatus Gould. Fig. 1.

Material.—662 part—a series of seven well-grown and well-furred young, apparently from the same litter and comprising four males and three females (length of head and body about 40 mm.); Maryborough, Queensland. M.5438 part—a series of seven litter mates, three males and four females (length of head and body about 27 mm.); Scone, New South Wales; coll. S. W. Jackson, 4th Jan., 1927.

Neither of the two groups is ideal for hair charting, the first being too far and the other not sufficiently advanced. The following comments are based on an examination of 662, but no noteworthy difference could be found between the two series.

The general hair current on the body may be described as primitive. There is a mid-ventral line of convergence on the neck which is caused by a medial trend in the

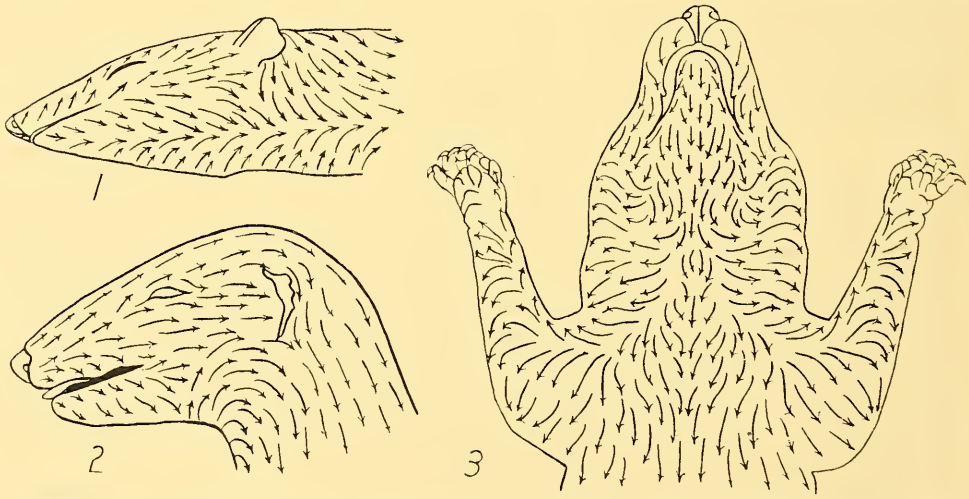


Fig. 1.—*Antechinus maculatus.* Lateral view of head and neck (specimen tilted to show gular field).

Figs. 2 and 3.—*Dasyurus quoll.* 2. Lateral view of head (auricle cut off close to head). 3. Ventral view of gular region and upper thorax.

hair direction between the mandibles in the vicinity of their angles and, caudal of this, a ventralwards sweep over the side of the neck of the hair immediately behind the base of the ear, this latter current almost reaching the mid-ventral line before turning caudomedially. Further back on the sides of the neck the hair direction is caudally and medially. On the abdomen, back from about half-way between the attachments of the limbs, there is a further tendency to mid-ventral convergent line formation brought about by a medialwards component in the caudal streaming of the hairs on the flanks. In the female this convergent line continues without interruption through the pouch area to the root of the tail. In the male it is interrupted by the occurrence of a prescrotal triangle, the base of which is about as wide as the greatest width of the scrotum, and runs transversely in front of its neck. The apex of the triangle, marked by a tuft, points cranially and lies on the mid-ventral line. The caudomedial flow of the general ventral body hair stops short at the sides of the triangle within which there is a field of shorter hairs running craniomedially. In the younger series (M.5438) the triangular area is naked.

Planigale ingrami Thomas.

Material.—M.6840—three males (length of head and body about 42 mm.); Connors Range, near Sarina, Queensland; pres. W. Tronson.

In every way similar to *Antechinus maculatus.*

Sminthopsis crassicaudata macrura Gould.

Material.—M.5214—one male and two females (crown-rump length about 21 mm.); Tamworth, New South Wales; pres. Mrs. W. G. Kennedy. M.2899—four males and one female (length of head and body about 30 mm.); Tamworth, New South Wales; coll. Rev. Dr. T. Porter, 9th Nov., 1920.

Both series are rather young for charting, especially of the posterior end. Neither shows evidence of differences in hair disposition from the account given above of *Antechinus maculatus*; the close similarity of the hair currents of the head and neck is clear; the hairs within the prescrotal triangle are not well developed in any of the males, but it would appear that their arrangement is the same.

Subfamily Dasyurinae.

Dasyurus quoll Zimmermann. Figs. 2 and 3.

Material.—Two females of equal size (length of head and body 150 mm., tail 92 mm.). 720A—New South Wales. M.5411—Sydney, New South Wales; pres. T. W. Cook.

Although the hair of both specimens is advanced beyond the point best for charting, what appears to be full description is still practicable. Its disposition is for the most part primitive. On the postaxial margin of the forearm there is a reversed stream which terminates in a convergent point just distal of the elbow; the reversal originates in a convergent interval immediately proximal of the wrist (cf. *Thylacinus*, fig. 7). The tracts on the throat are arranged in an unusual manner. On the chin and between the mandibles as far back as midway between the angle of the mouth and the angle of the mandible (that is, shortly behind the interramal papilla) the flow is directly caudad. Ventrally on the throat, the hairs continue to flow back on to the chest between two lines joining the cranial portion of the axilla on each side to the mid-ventral point on the caudal margin of the area just defined. Lateral of the triangle thus formed the hair on the throat flows outwards and backwards over the side of the face ventral of the level of the ear, the side of the neck, and on to the shoulder and upper arm. Where this upward stream encounters the caudalwards flow of the face there is a convergent hair-ridge which runs from just below the genal papilla to the lowest point of the base of the ear. Another short ridge is formed along the mid-lateral longitudinal line of the neck, behind the lower part of the base of the ear, where the back-flowing hairs running between the ears and round their bases meet the upwards flow from the side of the neck. The beginning of this ridge is marked by a convergent interval.

On the ventral abdomen, cranial of the level of the inguinal folds, the hair is directed straight back so that a mid-ventral convergent line or ridge is absent; within

the margin of the inguinal folds the hair direction becomes medial and caudal, resulting in the formation of a ridge in front of the pouch and between the pouch and the cloacal hillock.

Sarcophilus harrisii Boitard. Fig. 4.

Material.—A.6437—a female (length of head and body 147 mm., tail 42 mm.), A.6438—a male (length of head and body 145 mm., tail 40 mm.); Tasmania; coll. Kendall Broadbent.

The primitive head to tail hair trend is interrupted in only two regions of the body:

(i). At the side of the neck there is a convergent ridge on a line running between the ventral limit of the base of the ear and a point somewhat dorsal of the shoulder; it includes a convergent interval at about the middle of its course, so that in its cranial half the hair direction is towards the head, in its caudal half towards the shoulder. This arrangement is brought about by a fanning out of the backwardly directed currents on the throat and lower face behind the level of the genal papillae and a similar behaviour of the hairs on the dorsal half of the neck between and behind the ears which results in their meeting along the line indicated. Immediately behind the ear both currents bend forwards when nearing the ridge so that about half-way along it there is formed the convergent interval described.

(ii). Ventrally on the flanks and over part of the inguinal fold, the caudal flow sweeps round towards a mid-ventral convergent point about midway between the attachment of the limbs.

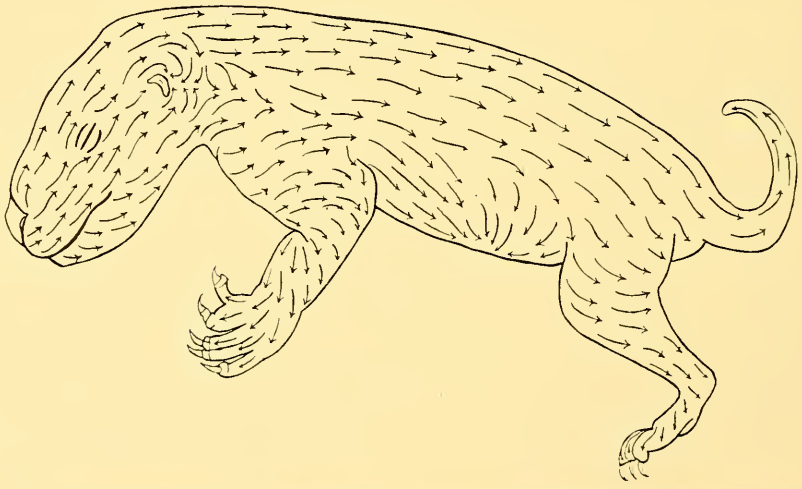


Fig. 4.—*Sarcophilus harrisii.* Lateral view of whole body (auricle cut off close to head).

Subfamily Thylacininae.

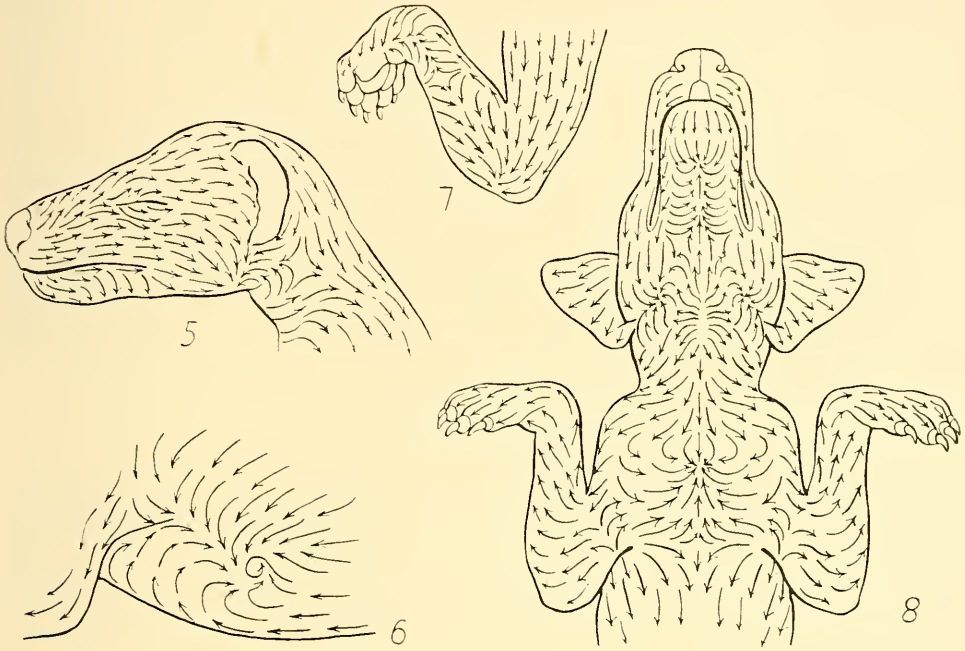
Thylacinus cynocephalus Harris. Figs. 5–8.

Material.—762—a female (length of head and body 288 mm., tail 119 mm.); Tasmania; coll. George Masters.

Head and neck.—Above the level of the oral fissure the hair on the head has an uninterrupted caudalwards flow, except between the eye and the ear, where it curves downwards to merge with a corresponding stream which flows round the base of the ear; the augmented stream thus formed converges on a point approximately over the angle of the jaw. On the throat and sides of the neck the hair tracts are arranged in a complicated manner. The flow on the chin, submental zone, and along the line of the lower lip is directly caudalwards. Elsewhere between the mandibles in front of a transverse line joining the angles of the mouth and passing through the interramal papilla, the flow is medially towards the mid-ventral line, a mid-ventral convergent ridge

being formed between the submental zone and the interramal papilla. The remainder of the gular region lying between the mandibles has a reversed stream.

Along the mid-ventral line of the neck a spindle-shaped area of divergence (having for most of its length the characteristics of a parting) gives rise cranially to the reversed stream between the mandibles, caudally to the backward flow on the upper chest, and from its sides originates a lateral and caudal stream which flows upwards over the side of the neck and shoulder to merge with the general caudalwards body current; towards the cranial end of the divergent area some of the hairs run laterally and then curve forwards joining the current mentioned above as flowing round the back of the base of the ear.



Figs. 5-8.—*Thylacinus cynocephalus*. 5. Lateral view of head and neck. 6. Right flank showing the centripetal whorl. 7. Forearm from the lateral aspect. 8. Gular region, thorax and fore-limbs.

The encounter of the opposing territories on the sides of the neck gives rise to a quadrilateral convergent interval having its diagonal on an oblique line which passes from the lower limit of the base of the ear backwards towards the mid-dorsal line through a point somewhat dorsal of the shoulder; there is a short hair-ridge between the interval and the shoulder. A further ridge occurs along the line joining the convergent point over the angle of the mandible and the interramal papilla; this is due to the meeting of the reversed tract on the throat with the caudal and caudomedial flow from the vicinity of the angle of the mouth; a divergent interval, nearer to the interramal papilla, is formed on the ridge.

Trunk.—Mid-ventrally on the upper chest about 15 mm. below the level of the shoulders a convergent point occurs towards which hairs flow from the root of the neck and diagonally across the chest from the medial half of the front of the upper arm and the more cranial portion of the axilla. Hairs also flow from the remainder of the axilla towards the mid-ventral line and, turning cranialwards just before reaching it, form a weak convergent ridge, the hair direction of which is towards the convergent point. At about the level of the junction of the posterior axillary fold with the body, there is a mid-ventral convergent area caudal of which the hairs stream back over the lower chest and on to the abdomen. The hair on the trunk in front of the inguinal region calls for no further comment beyond recording the presence of a pair of centripetal whorls about

10 mm. from the mid-ventral line and 15 mm. or thereabouts cranial of the inguinal fold. These whorls (clockwise on the left side, counter-clockwise on the right) are formed by a downward and forward curve of the main trunk tract on the flanks and an outward and forward sweep on each side of the ventral stream at that level; there is a weak line of convergence between these two components along a line running from just beyond the cranial end of the inguinal fold to the medial side of the whorl.

The epidermis between the thighs has been adversely affected by deterioration or abrasion, so that the arrangement of the tracts is decipherable only with difficulty. Outside the margin of the pouch, towards its cranial end, there is on each side a divergent centre (no whorling could be detected) from which hairs stream forward (to join those previously mentioned as entering into the composition of the centripetal whorl on the flank and its associated convergent ridge), laterally on to the inner face of the thigh, and caudally and laterally towards the posterior end of the body where they merge with another caudal and lateral stream which originates from a parting running between the pouch and the cloacal hillock. On the postaxial margin of the thigh, where this last current meets that on the lateral surface, a distinct hair-ridge is formed. Immediately in front of the pouch a reversed stream runs forward to meet the caudalwards flowing stream of the ventral abdomen and merges laterally with the reversed flow from further back.

Limbs.—On the lateral aspect of the forearm, just proximal of the wrist and near the postaxial margin, there is a convergent interval, and just distal of the elbow and also near the postaxial border, a convergent point; the interval between these two landmarks is occupied by a reversed flow to which hairs from both borders of the limb contribute.

The hind-limb shows no deviation from the primitive arrangement.

Family Peramelidae.

Isoodon obesulus Shaw and Nodder. Fig. 9.

Material.—M.6514—a male (length of head and body 110 mm., tail 55 mm.), M.6515—a female (length of head and body 115 mm., tail 54 mm.); Albany, Western Australia; pres. F. R. Bradshaw.

The primitive direction of the hair is in this species interrupted by reversals in three areas—on the throat, along the postaxial border of the forearm, and in the inguinal

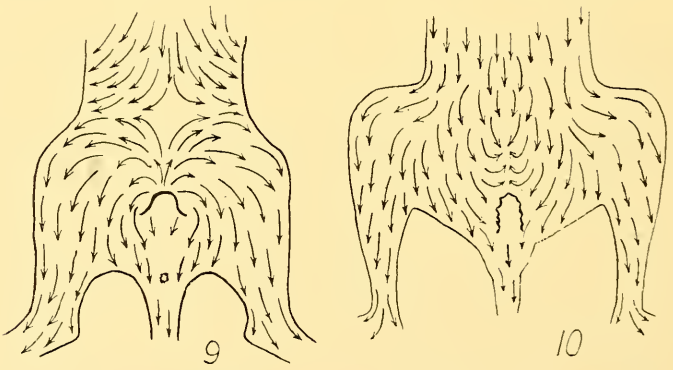


Fig. 9.—*Isoodon obesulus.* Hair tracts in the vicinity of the pouch.
Fig. 10.—*Perameles myosura notina.* Hair tracts in the vicinity of the pouch.

region. On the lower chest and upper abdomen the hairs on the ventral surface diverge from the mid-ventral line (without, however, forming a parting) to merge with the caudalwards flow on the flanks.

The throat reversal is similar in type and extent to that previously described in *Perameles nasuta* (Boardman, 1943, p. 139, fig. 1A). In this species, however, it differs in taking origin in a single asymmetrically placed whorl at the root of the neck—on

the left side and clockwise in the male, on the right side and counter-clockwise in the female.*

The reversal on the postaxial border of the forearm, with its associated convergent point distal of the elbow and convergent interval proximal of the wrist, is the same as that found in *Perameles nasuta* and *Isoodon barrowensis* (Wood Jones, 1922).

The inguinal reversal is similar in both sexes. It commences in front of the scrotum and pouch, respectively. Hairs stream forward and recurve to flow across the medial surface of the thigh, encircling the attachment of the stalk of the scrotum and margin of the pouch, as the case may be. The portion of the current which originates near the mid-ventral line recurves on to the inguinal fold and merges with the caudal and lateral flow from the ventral surface of the upper abdomen; mid-ventrally the boundary of these two opposing tracts is marked by a divergent interval.

Isoodon macrourus Gould.

Material.—M.6620—a male (length of head and body 110 mm., tail 49 mm.); Cape Arnhem area, Northern Territory; pres. Rev. W. S. Chaseling.

The disposition of the hair is in this species identical with that recorded for *Perameles nasuta* (*v. infra*). The pair of whorls described as occurring ventrally (Boardman, 1943, p. 139, fig. 1A) just above the root of the neck are in *macrourus* blurred in their formation, especially the one on the left side; the right member is placed slightly further caudally.

There is no mid-ventral line of convergence, the hairs on the ventral surface of the trunk flowing towards the flank and inguinal fold, as described above in *obesulus*. The reversed inguinal field is similar to that found in the male *obesulus*.

The hair generally is better developed on the left side than on the right.

Isoodon torosus Ramsay.

Material.—M.4227—a male (length of head and body 135 mm., tail 63 mm.); Macpherson Range, Queensland; coll. S. W. Jackson.

This specimen agrees closely with the male of *obesulus* (*v. supra*). The single gular whorl (counter-clockwise) is on the right side.

Perameles myosura myosura Wagner.

Material.—440½—a female (length of head and body 138 mm., tail 67 mm.); Salt R., south-west Australia; coll. George Masters.

The hair growth is too far advanced for detailed charting. The gular field is reversed in a manner similar to that described in *Isoodon obesulus* (*v. supra*); the reversal originates in a whorl on the right side as in the male *I. torosus* and in the female *I. obesulus*. A forearm reversal is present but there is no evidence (see, however, the subspecies *notina* below) of reversal on the ventral surface of the trunk where the hairs flow uninterruptedly on to the medial aspect of the thigh and round the margin of the pouch behind which they converge towards the mid-ventral line.

Perameles myosura notina Thomas. Fig. 10.

Material.—M.4978-9—two females of similar size (length of head and body 98 mm., tail 43 mm.); Ooldea, East-west Line, South Australia; coll. E. Le G. Troughton and J. H. Wright, 10th Oct., 1921.

The subspecies *notina* shows hair disposition very similar to *myosura*. There is only a single asymmetrically placed whorl on the neck, clockwise and on the left in one specimen, counter-clockwise and on the right in the other; the whorl is placed further cranially than in other species.

Both of these specimens are at an ideal stage for charting the hair currents of the groin. The general flow is caudalwards round the pouch towards the root of the tail as recorded for the subspecies *myosura*. In front of the level of the pouch, on each side of the mid-ventral line, the hair-flow is for a short distance bowed away from the medial

* The Australian Museum Collection contains a male *Isoodon* probably *obesulus* (unregistered—no data; length of head and body 135 mm., tail 56 mm.) which agrees point for point with the male of *obesulus* described above, but has two whorls at the root of the neck as originally described for *Perameles nasuta*.

line and the innermost hairs of this area recurve towards the mid-ventral line immediately in front of the pouch, giving rise to a restricted reversed field. The cranial limit of the reversal is marked by a convergent point where the caudalwards flowing hairs in front are encountered.

Perameles nasuta Geoffroy.

Material.—Unregd.—two females (length of head and body 120, 125 mm., tail 61, 63 mm., respectively); locality unknown.

One shows only a single gular whorl (counter-clockwise) on the right side whilst the other has the pair as described in an earlier communication (Boardman, 1943, p. 139, fig. 1A). Both have a reversed field ventrally, immediately in front of the pouch, as described above in *Isoodon obesulus*.*

Echymipera cockerelli Ramsay. Fig. 11.

Material.—M.3358—a female (length of head and body 137 mm., tail 43 mm.); Kaimare, Gulf of Papua, Papua; coll. A. R. McCulloch, 19th Oct., 1922.

This fine specimen has the reversed gular field originating in a single clockwise whorl on the left side. The growth of the hair is fairly advanced and shows the development of a clear lateral demarcation of the gular field from the backwardly directed facial tract due, apparently, to the more rapid growth and hispid nature of the hair on the side of the face (*cf. Isoodon barrowensis* as described by Wood Jones, 1922, p. 39, fig. 2).

There is no forearm reversal. The primitive arrangement is followed in the rest of the body.

Suborder Diprotodontia.
Family Phalangeridae.
Subfamily Tarsipedinae.

Tarsipes spenserae Gray. Fig. 12.

Material.—M.3153—two males probably litter mates (crown-rump length 24 and 25 mm.), M.3154—a female (crown-rump length 19·5 mm.); Nannarup, near Albany, Western Australia; coll. Hugh Leishman. M.3329—a female (crown-rump length ca. 26 mm.); Bornholm, near Albany; pres. David Morgan.

The dorsal and lateral aspects of the head, neck and trunk, and the limbs show the primitive caudalwards hair-flow; mid-dorsally on the snout from just caudal of the margin of the rhinarium back to about the level of the anterior angle of the eye, a convergent hair-ridge is present caused by a medial trend in the hairs between the large raised mystacial zones. Ventrally, from just cranial of the level of the flexure of the elbow back to the cloacal hillock, the hair direction is caudal and towards the mid-ventral line resulting in the formation of a weak medial hair-ridge. In front of the scrotum there is a reversed triangle similar to that described in *Antechinus maculatus*; a similar tendency to reversal occurs in front of the pouch but it is not well marked.

The throat and upper part of the chest show considerable variation from the primitive arrangement. At the root of the neck immediately in front of the shoulder on each side there is an imperfectly formed whorl (clockwise on the left, counter-clockwise on the right) from which hairs stream dorsally and caudally across the side of the neck, along the lateral aspect of the upper arm, and across its preaxial margin to flow medially and caudally towards the mid-ventral line of the chest, and medially and somewhat cranially across the throat ventrally. Behind the angle of the mouth the hairs of the caudalwards facial stream recurve on to the throat to flow medially and cranially towards its mid-ventral line. Beneath the base of the ear, on the line joining the angle of the mouth and the front of the shoulder, there is a divergent interval caused by the meeting of the back-flowing current of the face and the cranially directed hairs of the neck whorl.

In the female M.3329 and one of the two males of M.3153 the submental hairs flow cranially and medially, forming a weak medial convergent ridge, but in the remaining

* My previous reference to the hair tracts in *Perameles nasuta* is incorrect with reference to the ventral surface of the trunk; a re-examination of the specimen shows that, although extensively damaged, the same characteristics are present as in the two females now before me.

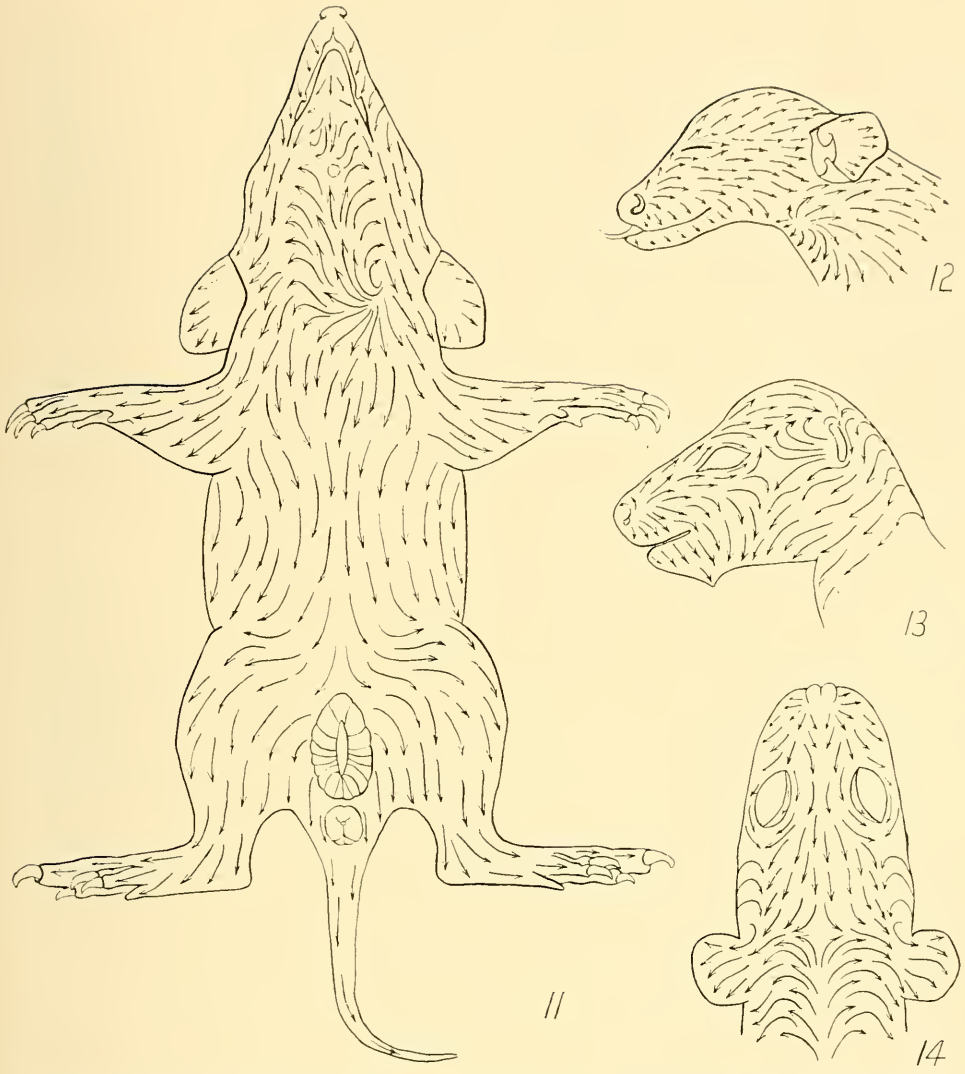


Fig. 11.—*Echymipera cockerelli.* Ventral view of body to show the general distribution of the hair tracts.

Fig. 12.—*Tarsipes spenserae.* Lateral view of head and neck.

Figs. 13 and 14.—*Dactylopsila picata.* 13. Lateral view of head and neck (auricle cut off close to head). 14. Head from above.

male of M.3153 the flow is caudal and medial. M.3154 is insufficiently developed to give information on this point.

Subfamily Phalangerinae.

Acrobates pygmaeus Shaw.

Material.—M.4197—two males and a female apparently litter mates (all within a millimetre or so of head and body length 39 mm., tail 30 mm.); Wingham, New South Wales; pres. T. Soper.

The hair direction is primitive throughout. On the ventral surface generally the flow is caudally and towards the mid-ventral line resulting in the formation of a mid-ventral convergent ridge on the throat, between the scrotum and the cloacal hillock, and between the cloacal hillock and the root of the tail.

Dactylopsila picata Thomas. Figs. 13 and 14.

Material.—M.535—a male (length of head and body 150 mm., tail 107 mm.); Herberton district, Queensland; coll. Cairn and Grant.

Head and neck.—The general trend of the hair on the dorsum of the head is caudalwards back to a transverse line running between the front of the bases of the ears; the middle of this line is marked by a divergent interval. There is a narrow area of reversal adjoining the caudal margin of the rhinarium. On the side of the face cranial of the eye the hair-flow is caudally and downwards; this current is continued back across the lower eyelid, and below, in front of the genal papilla, bends down to proceed almost transversely towards the interramal papilla. The portion flowing to the throat merges at the level of the genal papilla with a reversed flow from behind the base of the ear and side of the neck.

From the whole of the front of the base of the ear a reversed tract takes origin, the hairs of which fan out somewhat as they proceed. The lower portion of this reversal, opposite the genal papilla, flows forward and downward towards the throat merging beneath the genal papilla with the recurved current from the side of the snout. The remainder sweeps forward, upward, and backward in the area between the ear and the eye forming with the head flow just behind the level of the eye a short convergent ridge. The more dorsal hairs from the preauricular reversal merge with the backward flow on top of the head.

The arrangement of the hair on the neck is modified by the occurrence of a clockwise mid-dorsal whorl in line with the shoulders. From it hairs proceed caudally along the mid-dorsal line of the back, caudally and laterally over the root of the neck, the shoulder, upper arm and dorsal chest; in front, hairs stream forward to encounter the caudalwards flow on the top of the head forming the divergent interval mentioned above as occurring between the ears. Behind the divergent interval the cranialwards current from the whorl recurves to flow back round the base of the ear and on to the side of the neck, on the ventral surface of which it runs forward towards the interramal papilla. On the throat a mid-ventral convergent interval occurs at the root of the neck between the shoulders; it is caused by the hair-flow towards the middle line, over the shoulders and side of the neck, curving backwards on to the chest, and the hairs in front of this curving forward to run cranially and ventrally towards the interramal papilla. On the gular region and upper chest (except opposite the axilla) a mid-ventral convergent hair-ridge extends forward to the interramal papilla.

The hairs on the chin and submental region are dense, directed caudally, and converge behind on the interramal papilla, forming with the reversed throat tract, a well-defined convergent point.

Trunk and limbs.—The primitive arrangement is almost uninterrupted throughout the rest of the body. On the trunk the flow is ventrally and caudally towards the middle line where, below the level of the axilla, a weak convergent ridge is formed which continues back to the scrotum.

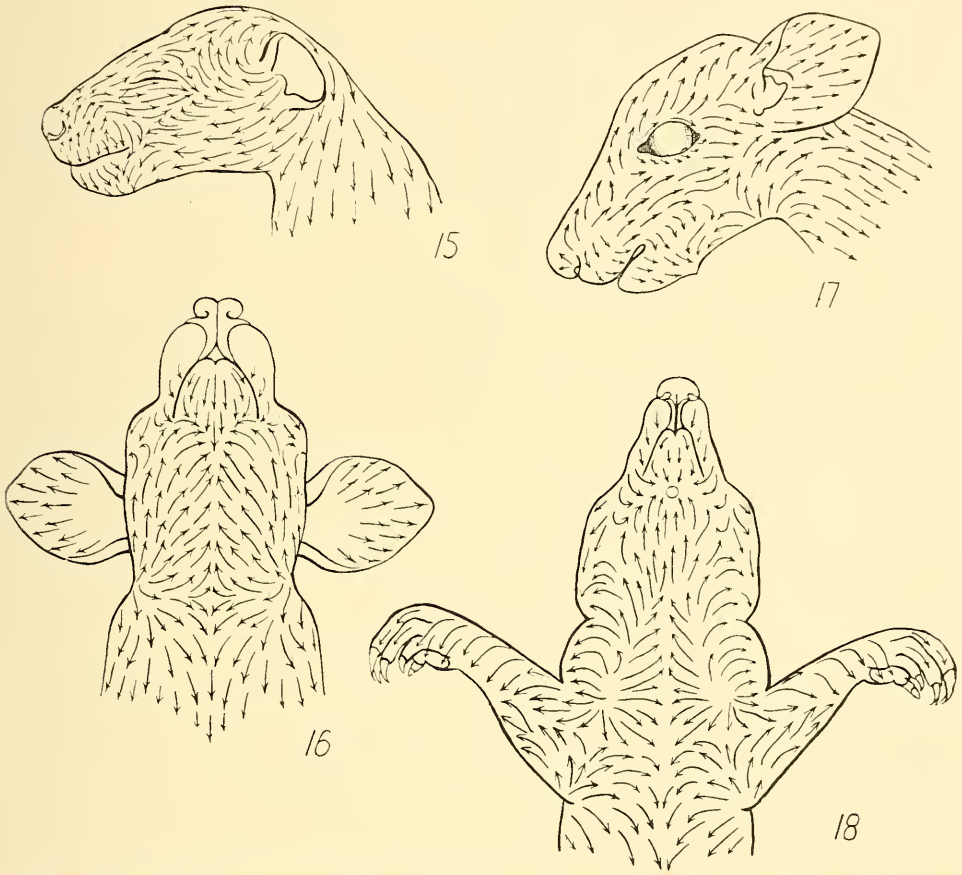
The current of hair flowing over the upper arm and flexure of the elbow encounters the divergent flow from the axilla (its point of origin is approximately the elbow) to form a short convergent ridge just within, and about parallel to, the anterior fold of the axilla (cf. *Bettongia penicillata*, fig. 18).

Schoinobates volans Kerr. Figs. 15 and 16.

Material.—M.3166—a male; Myall Lakes, New South Wales; coll. W. Barnes and H. Burrell, 1st Sept., 1922. A.10628—a male; Dawson R., Queensland; pres. Masters and Barnard. M.3002—a female; Wyong district, N.S.W.; pres. J. H. Wright. M.3036—a female; Dungog district; coll. A. Musgrave, 28th Sept., 1921. These four specimens are all about the same size—length of head and body, 160–165 mm., tail 185–210 mm.

Head and neck.—The head and neck present a complicated arrangement of hair tracts which, on analysis, is resolved into the impact on the primitive caudalwards flow of a strong reversed field. The reversal has two components—(*a*) a tract which diverges from the backward flow between the ears to sweep round behind the base of the

ear and thence forward over the side of the face towards the angle of the mouth and forward and ventrally on to the throat, and (*b*) a preauricular forward flow; no dividing line occurs between the two components except at the base of the ear where there is a tendency to the formation of a short hair-ridge along the line of the current. The sphere of influence of the reversed flow is demarcated by a linear convergent ridge passing from the angle of the mouth, obliquely across the face, to a point just behind the lateral angle of the eye; the caudal border of the submental region is continuous with this line.



Figs. 15 and 16.—*Schoinobates volans*. 15. Lateral view of head and neck (auricle cut off close to head). 16. Gular field and upper chest.

Figs. 17 and 18.—*Bettongia penicillata*. 17. Head and neck from the side. 18. Gular region, thorax and fore-limbs.

The confluence of the flow of hair over the upper and lower eyelids results in the formation behind the lateral angle of a very short hair-ridge. Between the posterior end of this ridge and the angle of the mouth there is the convergent ridge mentioned above; along its length, directly beneath the middle point of the palpebral fissure, a convergent interval is formed where the reversed current of the lower face divides to bend upwards towards the eye and downwards on to the throat, and where the tract which sweeps from between the mystacial zone and the eye over the side of the face below the palpebral fissure divides to give off below a band of hairs which proceeds towards the angle of the mouth. In its lower half the preauricular current flows straight forward parallel with the oral fissure; in its upper half it curves upwards and backwards round the upper portion of the base of the ear to merge with the caudalwards flow on the dorsum of the head. A convergent interval above and somewhat caudal of the lateral

angle of the eye is formed where the cranialmost hairs of the preauricular current recurve to flow into the short convergent ridge mentioned above as present caudal of the lateral angle. The hairs of the submental zone are directed straight back except near the angle of the mouth where they have a medial trend as well.

The arrangement of the hair on the dorsum of the neck is straight back; on its sides the hair flows ventrally and caudally on to the shoulder; in front towards the ear, the direction of flow changes gradually till it runs straight to the mid-ventral line (that is, at right angles to the long axis of the body); still further cranially it sweeps round the base of the ear and proceeds craniomedially over the angle of the jaw and on to the throat as the component (*b*) of the reversal described above. Mid-ventrally, from just behind the submental zone to a point on the upper chest about opposite the middle of the humerus, there is a convergent hair-ridge.

Trunk and limbs.—The hair on the remainder of the body is primitively disposed. There is no mid-ventral convergent ridge behind that mentioned as on the upper part of the chest; the hairs are short and generally directed straight back. Laterally on the trunk the hair sweeps backwards and laterally towards the free border of the membrane between the fore- and hind-limbs.

Family Phascolarctidae.

Phascolarctos cinereus Goldfuss.

Material.—483—a female (crown-rump length 111 mm.); Pine Mountains, south-east Queensland. 484—a female (crown-rump length 120 mm.); New South Wales.

The larger female shows no noteworthy difference from the condition described by Wood Jones (1923, p. 129) in the single specimen which he examined, except that the counter-clockwise whorled system, recorded as occurring mid-dorsally between the attachments of the fore-limbs, is in this specimen rather a divergent centre. In the other example (483) the hair is not well developed; it is of interest chiefly in that the dorsal whorl is double (clockwise on the right, counter-clockwise on the left) (cf. Boardman, 1943, p. 145).

Family Macropodidae.

Subfamily Potoroinae.

Bettongia penicillata Gray. Figs. 17 and 18.

Material.—1121—a male (length of head and body 165 mm., tail 145 mm.); Pine Mountains, south-east Queensland.

Head.—The general trend of the hair is caudalwards. On the head the backward flowing stream is split by the eye behind which it tends to converge and is again divided by the ear just above the level of the tragus. Following the caudal margin of the rhinarium between the nostrils there is a forwardly directed fringe of short colourless bristle-like hairs. A weak convergent hair-ridge runs forward from the ventral limit of the base of the ear towards the angle of the mouth where it terminates in a divergent interval on the side of the face beneath the lateral canthus of the eye; the ridge and the interval are formed by the confluence of a backwardly recurved stream from the throat with the flow on the side of the face.

Neck.—Dorsally the flow is caudalwards, laterally it is caudalwards and towards the mid-dorsal line, ventrally reversed (*v. infra*).

Trunk.—On the trunk generally the primitive arrangement is maintained, but in two regions there is a departure from this disposition:

(i). The first is in front of a line across the ventral aspect of the chest, drawn just within the cranial limit of the axilla. From the ends of this line there originates on each side a parting which is directed cranially and towards the mid-ventral line. Laterally from the parting, hairs recurve backwards over the shoulder, the side of the neck, and the lower portion of the face where they encounter the facial stream and form the oblique convergent ridge referred to above; medially the parting gives rise at first to hairs running caudally and medially, then medially for a short distance, further forward, medially and cranially, these last gradually changing to the fully reversed stream between the mandibles.

(ii). Between the scrotum and cloacal hillock there is a triangle of reversed hairs having its apex pointed towards the cloacal hillock.

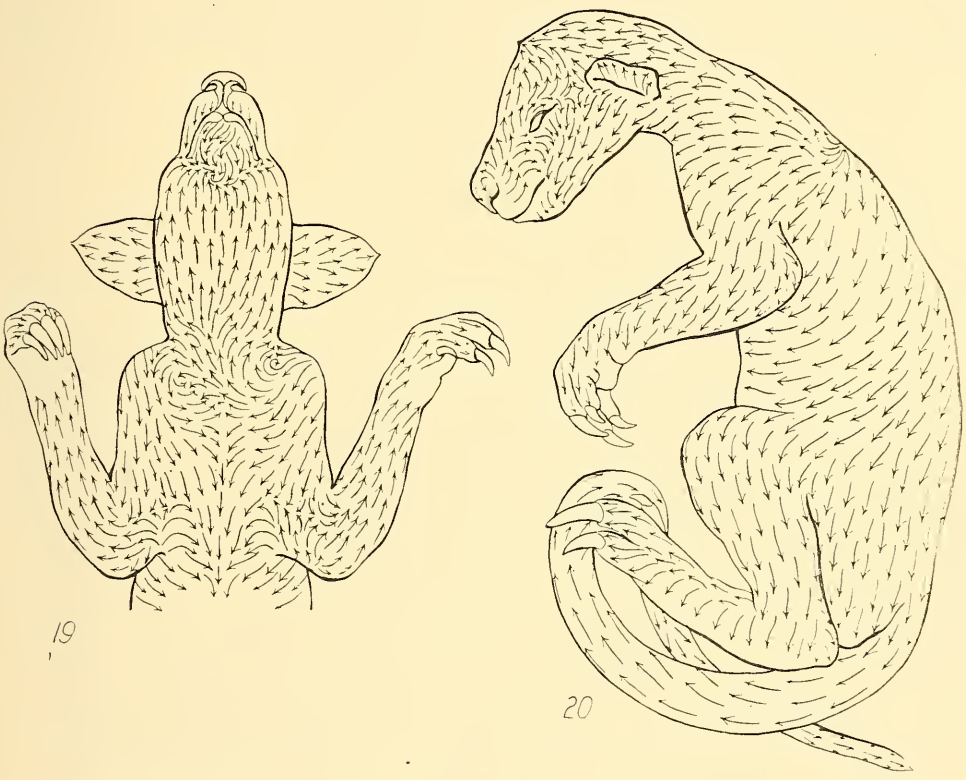
Limbs.—The hair direction on both fore- and hind-limbs is primitive except medially on the upper arm (Fig. 18).

Subfamily Macropodinae.

Dendrolagus inustus Schlegel and Müller. Figs. 19 and 20.

Material.—M.6214—a female (length of head and body 290 mm., tail 290 mm.); Aitape district, Sepik Division, Territory of New Guinea; pres. A. J. Marshall.

Head.—The presence of the same general ground plan found to occur in *Thylogale* sp. (*v. infra*) is evident, modified in accordance with the differing emphasis on its constituent currents. The lower part of the face, bounded dorsally by a line which appears as a backward continuation of the oral fissure, is clothed with a strong reversed current which flows forward from the side of the neck and is augmented above by forwardly directed hairs from the lower two-thirds of the front of the base of the ear.



Figs. 19 and 20.—*Dendrolagus inustus.* 19. Gular region, thorax and fore-limbs. 20. Lateral view of whole animal.

Neck.—All the neck hair is reversed.

Trunk.—Mid-dorsally on the back, just caudal of the level of the line joining the glenovertebral angle of the scapulae, there is a large clockwise whorl. From it, hairs stream cranially to the convergent point on the crown, caudally towards the tail, cranially and ventrally over the sides of the neck, shoulder and upper arm, ventrally towards the axilla, and caudally and ventrally over the sides of the lower chest and abdomen. On the flanks the backward and ventral stream of hair curves forward somewhat as it proceeds towards the mid-ventral line.

The arrangement of the hair on the ventral surface of the trunk is simple in comparison with the very complicated condition found in *Thylogale* sp. The cranial

and ventral flow over the shoulder and upper arm gives rise to the reversed flow on the upper chest and the root of the neck, and the caudally directed flow on the lower chest; an asymmetrical arrangement is produced in this region by the fact that the reversed flow mentioned is almost entirely produced by the current from the left side. The remainder of the undersurface of the trunk shows the primitive hair direction, viz., caudally and towards the mid-ventral line with a mid-ventral convergent hair-ridge.

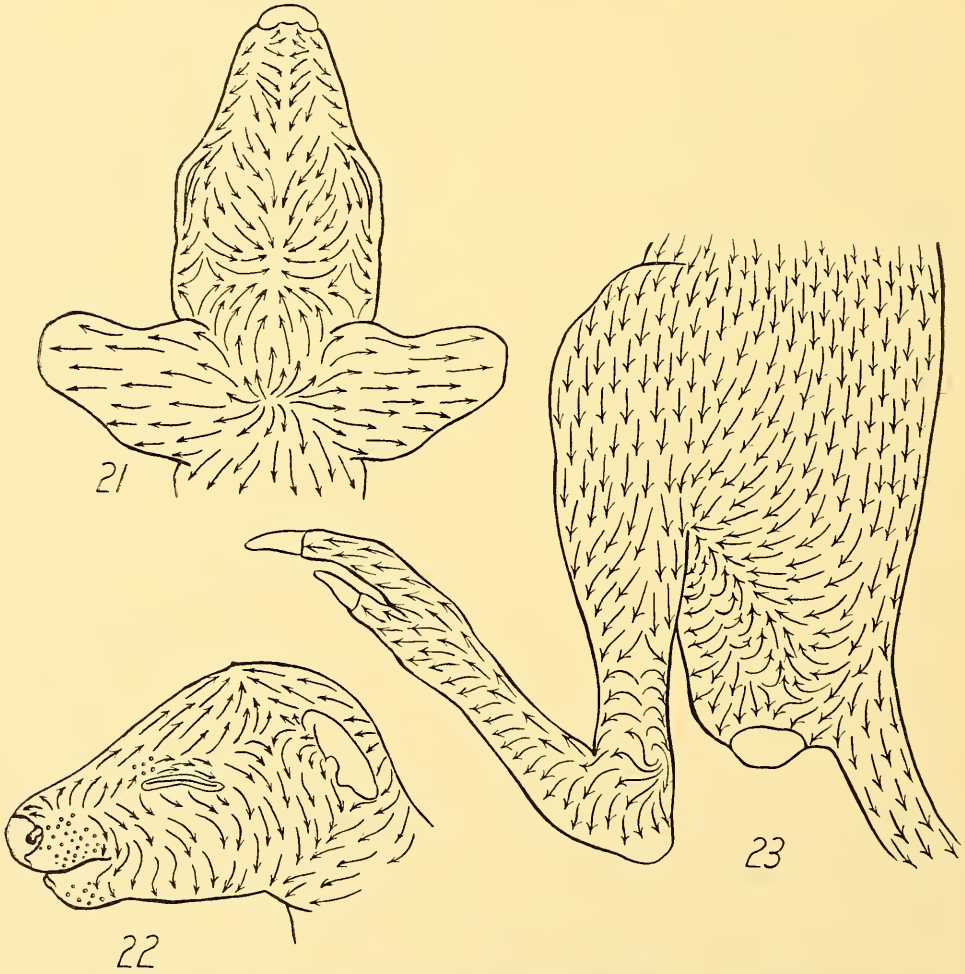
Limbs.—These call for no descriptive comment, the primitive hair disposition prevailing without interruption.

Thylogale sp. Figs. 21–24.

Material.—M.6667—a female (length of head and body 247 mm., tail 158 mm.); Bulolo R., Territory of New Guinea; pres. Dr. C. E. M. Gunther.

Head.—The arrangement of the hair tracts of the head is complicated. The territories, which are not clearly separable, will be considered from before backwards:

(i). The first is a reversed field, somewhat triangular in shape, having an irregular base line formed by the caudal margin of the rhinarium. The hairs are here more darkly pigmented than in the surrounding areas, and there are interspersed among them on each side of the mid-dorsal line four to six longer hairs (presumably tactile in function) shorter than, but similar to, the adjacent mystacials.



Figs. 21-23.—*Thylogale* sp. 21. Head from above. 22. Head viewed laterally (auricle cut off close to head). 23. Lateral view of hind end of body.

(ii). Between the mystacial zones and extending back to about half-way between their caudal limits and the medial canthus of the eye, there is a larger territory, not well separated from that in front, in which the hair direction is medial and caudal. A weakly defined ridge of convergent hairs occurs mid-dorsally through most of its length and extends slightly into region (i); the hairs, especially in its cranial half, are sparser than further back on the head.

(iii). Behind (ii) and the mystacial zones the caudally flowing stream on the face is split by the eye into a dorsal and ventral tract. The ventral tract sweeps back and curves downwards then forwards to contribute to the reversed flow on the throat. The

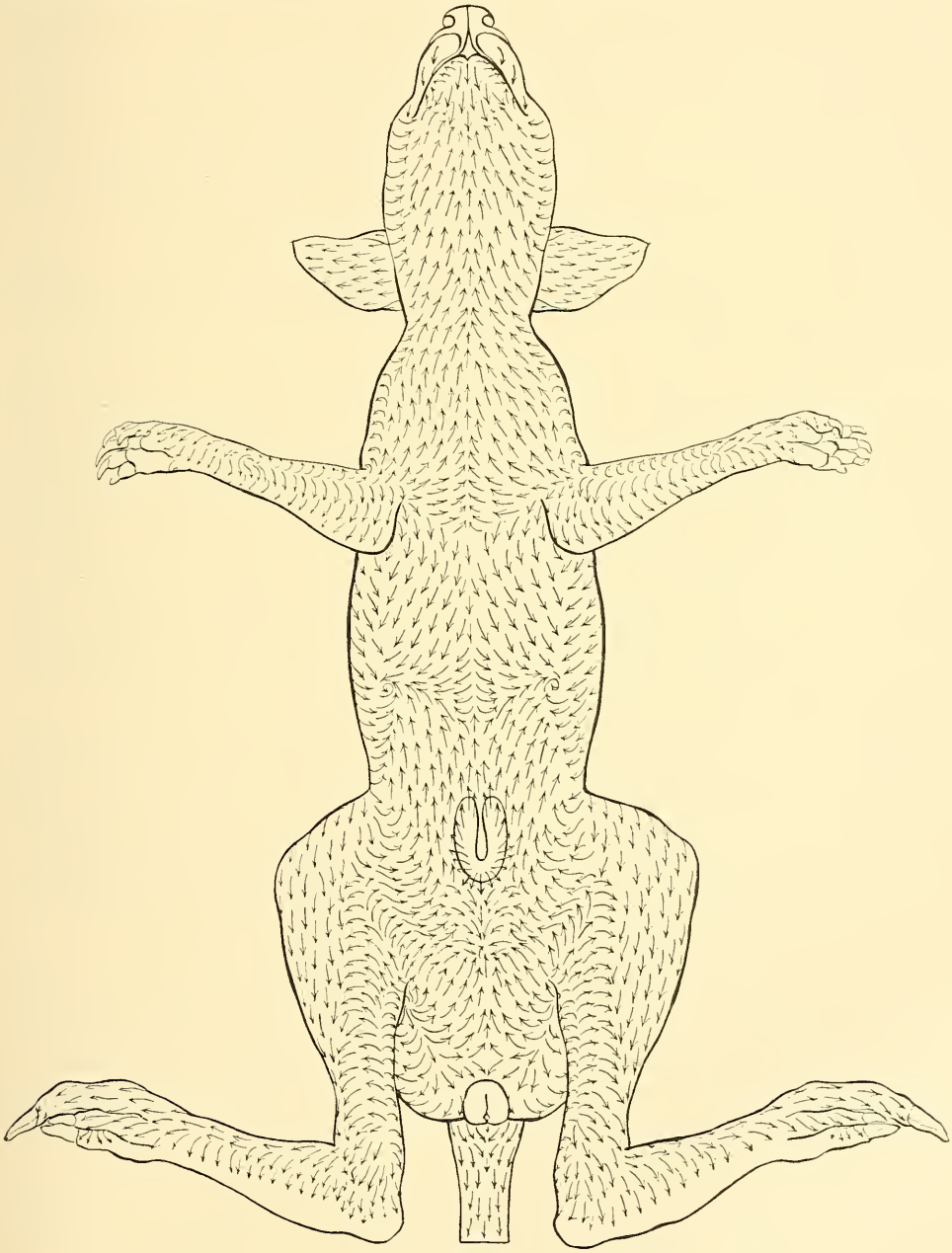


Fig. 24.—*Thylogale* sp. Ventral view of whole specimen.

dorsal tract is directed caudalwards and medially towards the convergent centre on the crown. A poorly developed parting is evident along a line joining the supraorbital papilla and the upper portion of the base of the ear; below, this parting gives rise to a stream which bends round the lateral canthus to join the flow proceeding to the throat from the face beneath the eye.

(iv). The remainder of the head and face except in front of the intertragal notch is covered with more or less completely reversed currents originating in the nuchal whorl or fanning out from the front of the base of the ear. The clockwise nuchal whorl has its centre just caudal of the mid-dorsal point of the nuchal crest between the bases of the ears. From it, hairs are directed cranially and medially towards the convergent centre on the crown, laterally on to the medial surface of the auricle and caudally over the dorsum and sides of the neck. A current flows round the base of the ear to form with the downward flow on the side of the face an oblique convergent ridge which extends from about opposite the antitragus to the angle of the mandible. From the front of the base of the ear, opposite to and dorsal of the tragus, hairs fan out forming a divergent interval with the currents from (iii). The line of demarcation between (iii) and (iv) may arbitrarily be drawn from the convergent centre on the crown to the divergent field just mentioned and thence vertically to the oblique convergent ridge beneath the ear.

A covering of short down, directed backwards and downwards, is interspersed among the mystacial vibrissae. Between the long sensory vibrissae the submental area is clothed with fine backwardly directed hairs, but on the throat between the mandibles the stream is reversed.

Neck.—Hair direction on the neck is modified by the presence of the nuchal whorl. Dorsally it is caudalwards. On the sides the flow curves round to join the reversed current on the throat, except for a narrow band in front of the shoulder which recurves over the shoulder on to the lateral aspect of the upper arm; this division of the stream is marked by a convergent interval, the ventral components of which are formed by a similar division of the reversed flow of the upper chest. Behind the interval, a convergent ridge is formed just lateral of the anterior margin of the upper arm and extending distally on the limb almost to the flexure of the arm; no ridge is present in front of the interval.

Trunk.—Dorsally on the back the hair-flow is directly caudally to the root of the tail. Laterally the hair trends caudally and ventrally; over the great trochanter of the femur and the tuberosity of the ischium the current curves round towards the postaxial aspect of the thigh.

The reversed field described as present on the throat is continued back on the upper chest to about half-way between the line of the shoulders and the epigastrium. It originates caudally in a diverging flow of hair from the axilla which proceeds medially before turning cranially; in the hind portion the current from the axilla runs caudally and medially before turning towards the head. The hair currents on the remainder of the chest and the upper part of the abdomen form a single area in which the direction is caudally and laterally away from the mid-ventral line; there is no hair-parting; the line of demarcation between this area and the reversed area above it is marked by a mid-ventral convergent interval.

The hairs on the lower abdomen back to the root of the tail present a series of tracts more or less merging into one another, but having differing directions of flow. The area under consideration is limited laterally by a well-defined line on which the caudally and ventrally directed hairs of the sides of the body give way to the differently directed currents of the ventral surface; this line of demarcation is continued back along the base of the hind-limb so that it marks off also the ventral tracts from those on the medial aspect of the thigh. For convenience the various areas are numbered from before backwards:

(i). A reversed tract (the flow of which is cranial and somewhat lateral) covers the abdomen in front of the pouch and extends caudally between the pouch and the base of the limb for a short distance beyond the caudal limit of the pouch. A mid-ventral divergent interval separates this area from that in front and the density of its hairs is

markedly less than in front. The lips of the pouch are fringed externally with radiating hairs, longer caudally.

(ii). Immediately behind the pouch there is a tract with the hair flowing caudally; this is bounded by the pouch in front, a transverse convergent ridge behind (which lies about half-way between the caudal margin of the pouch and the convergent interval in front of the cloacal hillock), and laterally by lines which appear to coincide with the underlying marsupial bones.

(iii). Behind (ii) and lateral of about its caudal quarter, and occupying the remainder of the ventral surface, there is a considerable area of varying hair direction, but for the most part reversed. This is the result of the influence of a centrifugal whorl behind the base of the hind-limb on each side; the whorl on the left is clockwise, that on the right counter-clockwise and from each there extends caudally and medially a feathering. The feathering laterally merges immediately with the reversals brought about by the curving round of the currents on the side of the body over the femur head and tuberosity of the ischium; medially the hairs mostly flow inwards and upwards, but some flow inwards and downwards towards the cloacal hillock giving rise to the convergent interval mentioned above as immediately in front of it.

The presence of pigmented hairs interspersed among the colourless ones enables the lateral limits of the areas just described to be separated easily from the denser but uniformly pale hairs of the medial aspect of the thigh.

Between the lower limit of (i) and the upper limit of (iii), a narrow zone of hairs occurs directed transversely in towards, and ending at the lateral boundary of, (ii); they appear to be a continuation of the sweep of hairs on the medial aspect of the thigh.

Fore-limb.—On the lateral surface of the limb the primitive arrangement of the hair holds, that is, distally and towards the preaxial border in the upper arm, distally and towards the postaxial border in the forearm. Medially on the forearm, at about where the distal third joins the proximal two-thirds, there is a whorl (clockwise on the left, counter-clockwise on the right) from which a feathering proceeds proximally up the limb and into the axilla, losing its identity in the radiating zone within the axilla which has been described above.

Hind-limb.—Laterally the leg presents the normal primitive arrangement over the broad thigh and proximal three-fifths of the shank; on the shank, where the distal two-fifths meet the proximal three-fifths, a divergent interval is caused by the downward current meeting an upward current in the form of a feathering which lies in the groove between the tendon of Achilles and the bone of the leg. The feathering has origin in a centrifugal whorl, the centre of which lies just above the swollen end of the fibula (the whorl on the left is clockwise, on the right counter-clockwise). In the corresponding groove on the medial aspect of the leg, a similar whorl (counter-clockwise on the left, indeterminate on the right) and feathering are present; these medial featherings persist further proximally than those on the lateral aspect. From somewhat proximal of the divergent interval a hair-ridge is formed along the postaxial margin by the confluence of the featherings; an anterior hair-ridge is not so well defined and occurs laterally near the preaxial margin. Medially on the thigh there is some interruption to the even flow over the knee by the extension forward of the sphere of influence of the whorl situated behind the base of the limb.

Wallabia bicolor Desmarest. Fig. 25.

Material.—930 part—a male (length of head and body 295 mm., tail 225 mm.); Pittwater, near Sydney, New South Wales.

Head and neck.—In this species the hair on the head in front of the vertex convergent point is poorly developed. The tract pattern on the head and neck follows closely the ground-plan described for *Thylogale* sp. (*v. supra*). The nuchal whorl is counter-clockwise and placed relatively slightly further back. The convergent interval, recorded in *Thylogale* as occurring ventrolaterally at the root of the neck, is in *W. bicolor* placed laterally on the neck about midway between the ear and the shoulder; no convergent ridges are apparent either in front of or behind it. Consequent upon the more dorsal position of this interval, the reversed stream of hairs on the side of the neck belonging to

the reversed throat stream plays the major part in the formation of the oblique convergent ridge running forward from the ear.

Trunk.—As in the head and neck, the principal features of the hair tracts of the trunk are common to both this species and *Thylogale*, except between the hind-limbs where there is a greater degree of simplicity.

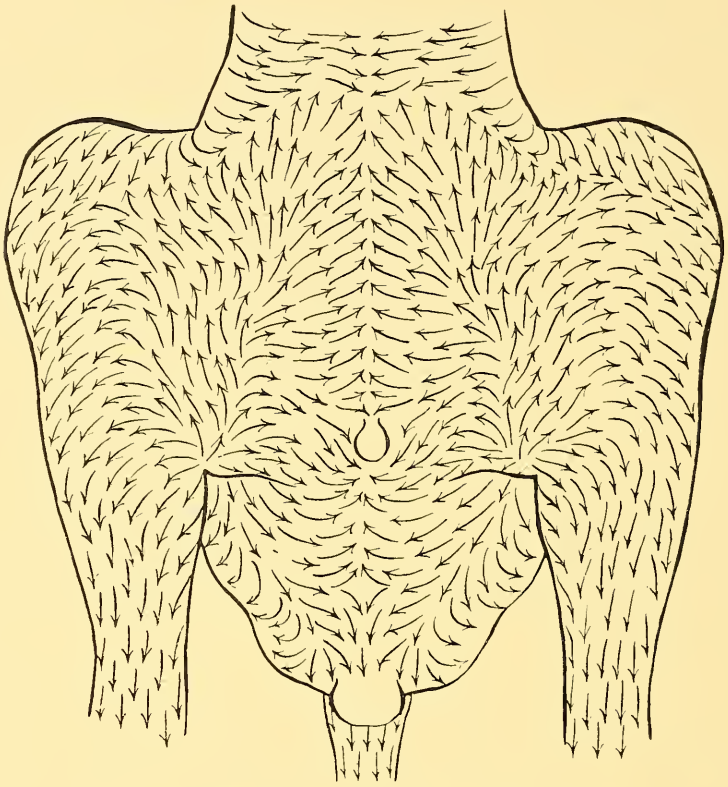


Fig. 25.—*Wallabia bicolor*. Hair tracts of the groin.

Some asymmetry is noticeable in the triangle included between the root of the tail, the head of the femur and the cloacal hillock. The curve of the hair current over the rump on to the posterior aspect of the thigh is not so well marked as in *Thylogale*; on the left side this curving gives rise to a clockwise centripetal whorl ventral of the head of the femur, but no similar structure is formed on the right side.

On the chest ventrally, the arrangement is the same as in *Thylogale*. The caudally flowing tract on the lower chest runs on to the abdomen and continues back to about the middle of the inguinal fold, that is, considerably further than in *Thylogale*; instead of proceeding caudally and laterally as in *Thylogale* the hair-flow in this part of *bicolor* is caudally and medially, resulting in the formation of a well-defined mid-ventral convergent ridge.

The pattern of the hair tracts between the inguinal folds and the attachments of the hind-limbs is shown in Figure 25.

Limbs.—The hair-flow is entirely primitive except on the medial aspect of the lower leg where the hair disposition is similar to that described in *Osphranter* below.

Osphranter robustus Gould.

Material.—A female (length of head and body 365 mm., tail 265 mm.); Gudgenby, Australian Capital Territory; coll. A. G. W. Bootes, July, 1939.*

* This specimen belongs to the collection of the Australian Institute of Anatomy, Canberra.

The hair on the specimen is at an advanced stage, but the tracts are still defined and readily described.

Head and neck.—There is practically point for point agreement with *Thylogale* except that a bilateral pair of nuchal whorls is present, that on the left being counter-clockwise, that on the right clockwise. The whorls are situated in line with the posterior margin of the attachment of the ears; between them and back for about the length of the neck a mid-dorsal convergent hair-ridge occurs.

Trunk.—The arrangement of the trunk hair follows that described for *Wallabia bicolor* which varies from the *Thylogale* plan in the greater simplicity of the ventral abdominal tracts.

There is no development of centripetal whorls on the rump. The specimen shows an interesting feature in the presence of a well-defined convergent ridge which runs vertically from over the head of the femur to the postaxial border of the thigh. It occurs as a result of the sharper curving round towards the postaxial margin of the thigh of the more dorsal hairs in front of the tail which thus encounter those below them along the line indicated. This type of ridge formation is most unusual.

As in *W. bicolor* the caudalwards flow on the lower chest and upper abdomen is back and towards the mid-ventral line, but a clear mid-ventral convergent line is absent; about midway between the attachments of the limbs a mid-ventral tuft or convergent point is present caused by a recurving of the tract on the flanks ventrally and cranially.

Limbs.—The primitive arrangement is disturbed only on the medial face of the lower limb where from the groove between the tendo Achilles and the leg bones hair flows distally and towards the preaxial margin and distally and towards the postaxial margin without, however, the intervention of a very well-defined parting.

Literature Cited.

Boardman, W., 1943.—On the External Characters of the Pouch Young of Some Australian Marsupials. *Aust. Zool.*, 10 : 138-160.

Gray, J. H., 1935.—The Hair Tracts of the Australian Aboriginal. *J. Anat.*, Lond., 69 : 206-225.

Iredale, T., and Troughton, E. Le G., 1934.—A Check-list of the Mammals recorded from Australia. *Aust. Mus. Mem.*, 6 : 101 pp.

Jones, F. Wood, 1920.—The External Characters of Pouch Embryos of Marsupials. No. 1. *Trichosurus vulpecula*, var. *typicus*. *Trans. Roy. Soc. S. Aust.*, 44 : 360-373.

————, 1922.—Id. No. 3. *Isoodon barrowensis*. Ibid., 46 : 39-45.

————, 1923.—Id. No. 5. *Phascolarctus cinereus*. Ibid., 47 : 129-135.

————, 1924.—On the Causation of Certain Hair Tracts. *J. Anat.*, Lond., 59 : 72-79.

————, 1925*a*.—The Mammalian Toilet and Some Considerations arising from It. *Pap. Proc. Roy. Soc. Tasm.*, 1925 : 14-62.

————, 1925*b*.—The Hair Pattern of a Kangaroo; a Study of Cause and Effect. *J. Mammal.*, 6 : 13-17.

————, 1927.—The Middorsal Hair Whorl of Man. *Amer. J. Phys. Anthrop.*, 11 : 89-95.

————, 1941.—Tension Lines, Cleavage Lines and Hair Tracts in Man. *J. Anat.*, Lond., 75 : 248-250.

————, 1943.—Habit and Heritage. London.

Kidd, W., 1903.—The Direction of Hair in Animals and Man. London.

————, 1920.—Initiative in Evolution. London.

Ride, L. T., 1932.—A Preliminary Report on Investigations into Certain Racial Characteristics of the Natives of British North Borneo. *The Caduceus*, 11 : 62-76.

Schwalbe, G., 1911.—Über die Richtung der Haare bei den Affenembryonen. Selenka, Studien über Entwickelungsgeschichte der Tiere, Bd. v, 205 pp.